Evolution of Feeding and Mating Behaviors in the Empidoidea (Diptera : Eremoneura)

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ABSTRACT

The phylogeny of the Empidoidea is discussed in relation to the works of ULRICH (1971), CHVALA (1983), WIEGMANN et al. (1993), CUMMING et al. (1995) and SINCLAIR (1995). The clade [Dolichopodidae + Microphoridae] + [Tricopezinae + Brachystomatinae + Ceratomerinae] is the sister group of [Atelestidae + Hybotidae + Empididae]. The family Empididae is assumed to be a monophyletic group on the basis of the presence of an endoskeletal pocket in line with the laterotergite (ULRICH, 1971, 1994), however this character is independently derived in the Tricopezinae and Ceratomerinae. The phylogeny is used to interpret the evolution of two ethological characters, feeding and swarming habits. Optimization of these attributes on the cladogram corroborated the hypothesis that predation is ancestral in Empidoidea. Mating swarms are found to be a specialized behavior for the subfamily Empidinae and non-homologous of swarms of some other empidoids. These optimizations and evolutionary pathways refute the traditional evolutionary models of swarming in the Empidoidea. Finally, the hypothesis that swarming is an adaptation for the meeting of sexes is corroborated for the Empidinae.

RÉSUMÉ

Evolution du régime alimentaire et du comportement reproducteur chez les Empidoidea (Diptera: Eremoneura)

La phylogénie des Empidoidea est discutée en relation avec les travaux d'ULRICH (1971), CHVALA (1983), WIEGMANN et al. (1993) et SINCLAIR (1995). Le clade des [Dolichopodidae + Microphoridae] + [Tricopezinae + Brachystomatinae + Ceratomerinae] est le groupe frère des [Atelestidae + Hybotidae + Empididae]. Les Empididae sont supposés former un groupe monophylétique sur la base de la présence d'une poche endosquelettique se situant dans le prolongement du latérotergite (ULRICH, 1971, 1994), cependant ce caractère est apparu par convergence chez les Tricopezinae et les Ceratomerinae. La phylogénie est utilisée pour interpréter l'évolution de deux caractères éthologiques, les comportements reproducteurs et alimentaires. L'optimisation de ces attributs sur le cladogramme corrobore l'hypothèse d'une origine ancestrale pour la prédation chez les Empidoidea. La formation d'essaims de reproduction est un comportement spécialisé des Empidinae qui n'est pas homologue avec les essaims formés par d'autres empidoïdes. Ces résultats réfutent les modèles traditionnels d'évolution des essaims chez les Empidoidea. Par contre, l'hypothèse d'une adaptation à la rencontre des sexes pour la formation d'essaims est corroborée pour les Empidinae.

INTRODUCTION

Species of Empidoidea present a large range of feeding, swarming and reproductive behaviors. Many studies of these ethological characters have been carried out and several

evolutionary hypotheses have been proposed (HAMM, 1908, 1909, 1933; ELTRINGHAM, 1927; KESSEL, 1955; DOWNES, 1970; TREHEN, 1971; CHVALA, 1976) but never on a strict phylogenetic basis. Nuptial gifts have been discussed by some recent authors (THORNHILL & ALCOCK, 1983) but herein I propose to study two other attributes: feeding and swarming habits.

Predatory habits and mating swarms have always been hypothesized as primitive habits in the Empidoidea (CHVALA, 1983), although mating swarms have only been observed in the subfamily Empidinae. Other empidoïds form swarms but mating behavior always takes place outside them. This point of view is traditional and deep-rooted.

Recent progress in the phylogeny of the Empidoidea allows me to test traditional hypotheses of this kind with respect to phylogenetic evidence. Evolutionary patterns of attributes – feeding and swarming habits – are inferred by mapping them on the phylogeny. These inferred patterns are compared afterwards to former evolutionary hypotheses.

MATERIALS AND METHODS

A character analysis (for thirteen taxa and fifteen characters) was performed on the families and subfamilies of Empidoidea using the program Hennig86 (FARRIS, 1988), results were analyzed with Clados, version 1.1 (NIXON, 1992). This paper does not focus on the phylogenetic tree itself, characters are thus presented in the appendix 1. Using "i.e." (implicit enumeration) algorithm, a tree was obtained with the length of 21 steps, the consistency index $CI = 0.80$ and the retention index $RI = 0.90$ (Fig. 2).

The evolution of attributes was inferred by optimization on phylogenetic trees, using Fitch parsimony (FITCH, 1971). States of attributes are coded and entered in the matrix and their optimization is viewed and analyzed by Hennig86 as non-additive, under the "xx" function, without outgroup and using "ccode]" function. Polymorphism between species or genera or within species in a terminal taxon is coded "?". Tree drawings were performed using Treeview (PAGE, 1996).

PHYLOGENETIC SYSTEMATICS

Historical

Among the Empidoidea (Fig. 1), five families were recognized by CHVALA (1983): Empididae, Hybotidae and Microphoridae (resulting of the division of the traditional family Empididae), Atelestidae (including some genera originally classified in the Platypezidae and Hybotinae) and Dolichopodidae. In the phylogeny which he proposed, the Empidoidea and Cyclorrhapha form a monophyletic group but the Atelestidae are the sister group of the Cyclorrhapha, thus the Empidoidea are paraphyletic. At the present time, the Empidoidea (including the family Atelestidae) are recognized as a monophyletic taxon supported by four synapomorphies (CUMMING *et al.*, 1995) and sister group of the Cyclorrhapha, forming together the clade Eremoneura supported by ten synapomorphies (MCALPINE, 1989; SINCLAIR, 1992; CUMMING *et al.*, 1995).

WIEGMANN *et al.* (1993) proposed some phylogenetic hypotheses and focused on the theories (epandrial and periandrial) of male genitalia evolution. Unfortunately, as SINCLAIR (1995: 719) noted, WIEGMANN's hypotheses are poorly supported, several characters being highly polymorphic and the others incorrectly scored.

SINCLAIR (1995) reduced the family Empididae (*sensu* CHVALA) to four subfamilies, Empidinae, Hemerodromiinae, Clinocerinae and Oreogetoninae. The Brachystomatinae, Ceratomerinae and Tricopezinae (The subfamily Tricopezinae was newly defined by SINCLAIR, 1995, its monophyly is supported by the presence of a median apodeme in the female
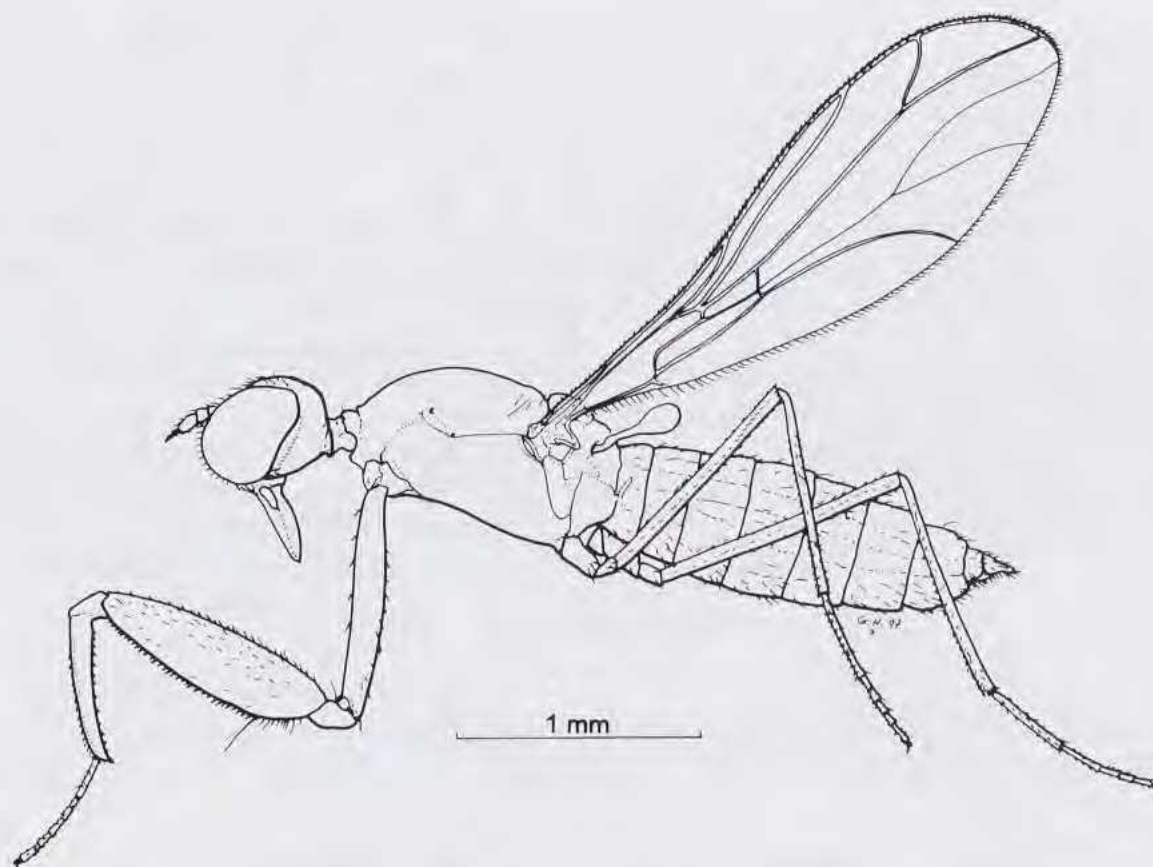
FIG. 1. — *Hemerodromia sp.* (from French Guiana), female, habitus. Scale bar = 1 mm.

postabdomen) are hypothesized to be a monophyletic taxon, sister group of [Dolichopodidae + Microphoridae] on the basis of several characters of female postabdomen largely detailed by SINCLAIR (1995: 718-719, characters 1, 2, 3 and 4; see also appendix 1, characters 11-14).

Characters

The works of ULRICH (1971), CHVALA (1983), WIEGMANN *et al.* (1993), CUMMING *et al.* (1995) and SINCLAIR (1995) have been re-analyzed to propose a matrix of 15 morphological characters (Appendix 1). The principal subject of this paper is not the phylogeny of the Empidoidea but the evolution of ethological characters, I refer readers to the original references for more details about the morphological characters. Nevertheless, at this point it is pertinent to comment of two of the characters.

Prokatepisternum fused with the basisternite (Character 3). Primitively, the basisternite (= prosternum), a sclerite located between the front coxae, is small and isolated, but in numerous taxa of Diptera it is developed laterally and fused with the anterior ventral episternum
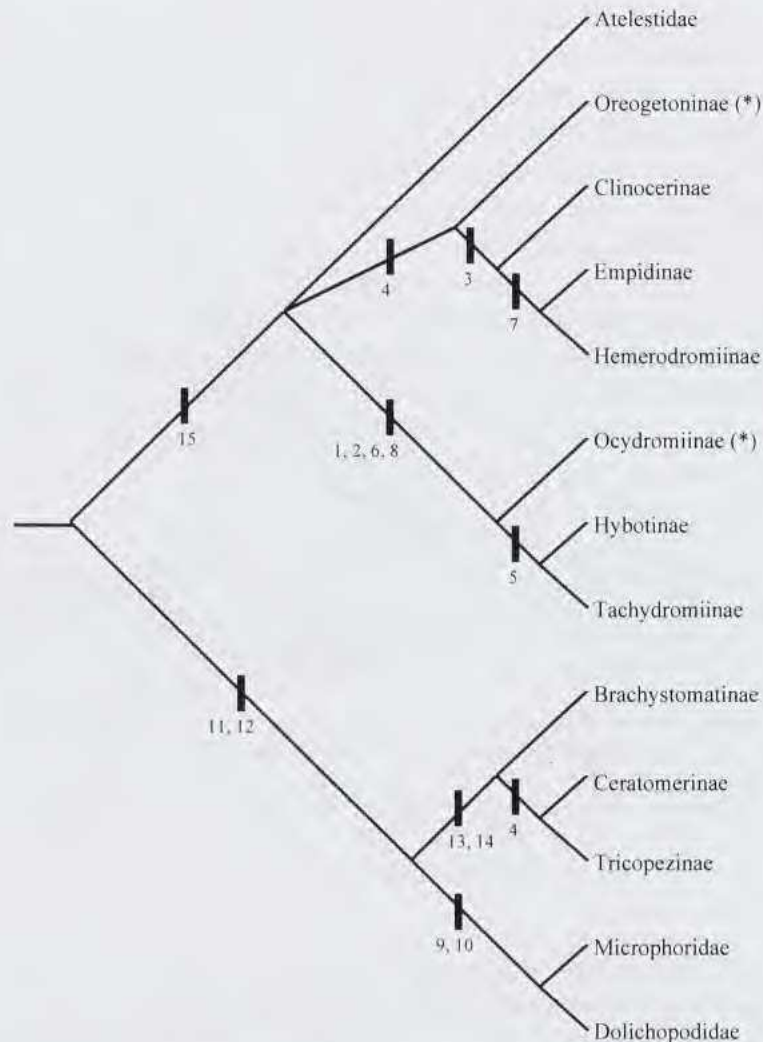
Fig. 2. — Cladogram of the families and subfamilies of Empidoidea, according to data presented in appendix 1 and treated as described in materials and methods. *: paraphyletic taxon.

(prokatepisternum) to form a precoxal bridge (SPEIGHT, 1969). This has been observed in the Empidinae, Hemerodromiinae, Clinocerinae, Brachystomatinae, Ceratomerinae, some Tricopezinae (at least *Heterophlebus*, *Hyperperacera* and *Heleodromia*), some Dolichopodidae and some Tachydromiinae.

Presence of an endoskeletal ridge in mesanepimeron (Character 4). ULRICH (1971) showed the existence of an endoskeletal ridge in mesanepimeron in some empidoïds, forming a characteristic complete or incomplete pocket in line with the laterotergite. It is curious that this character has never been used or commented by other workers since 1971. A complete pocket has been observed in the Oreogetoninae (ULRICH, 1994), Clinocerinae (*Wiedemannia*, *Dolichocephala*, ULRICH, 1971), Hemerodromiinae (*Chelipoda*, ULRICH, 1971), Tricopezinae (*Tricopeza*, *Rubistella*, ULRICH, 1971, 1994) and Ceratomerinae (ULRICH, 1994), whereas an incomplete pocket seems present in all species of the subfamily Empidinae, and some

Tricopezinae (at least *Heterophlebus*). Consequently this character has been used in the matrix (Appendix 1) under 3 states and treated as non-additive.

Phylogeny: Empididae as a monophyletic group (Fig. 2)

The monophyly of the Empididae is supported by the presence of an endoskeletal ridge in the mesanepimeron forming a complete pocket in line with the laterotergite even if this pocket is secondarily reduced dorsally (Empidinae) or entirely lost in the more specialized Hemerodromiinae like *Chelifera* where the lengthening of thorax has led to the loss of pleural sutures. It is hypothesized that the presence of the pocket is a synapomorphy for the clade [Oreogetoninae + Clinocerinae + Hemerodromiinae + Empidinae]. A pocket of the same structure and position existing in Tricopezinae and Ceratomerinae, it is provisionally supposed that these two taxa are sister groups.

Within the clade [Atelestidae + Hybotidae + Empididae], supposed monophyletic on the basis of the absence of acanthophorites in the female (SINCLAIR, 1995), only the Clinocerinae, Hemerodromiinae and Empidinae (and also a few species of Tachydromiinae) possess a precoxal bridge. Consequently, these three subfamilies form a monophyletic group within the Empididae. A precoxal bridge has appeared independently once or several times in the clade [Dolichopodidae + Microphoridae + Ceratomerinae + Brachystomatinae + Tricopezinae].

THE ATTRIBUTES

Feeding habits

Most Empidoidea are predators, however some are also flower visitors (pollen or nectar feeders). Table 1 shows the different feeding habits observed in the superfamily. Two subfamilies

TABLE 1. — Feeding habits in the Empidoidea. A question mark indicates an unknown state.

Taxa	Predators	Nectar or pollen feeders
Atelestidae	?	?
Oreogetoninae	in flight	x
Clinocerinae	in flight	
Empidinae	in flight	x
Hemerodromiinae	on solid substratum	
Ocydromiinae	in flight	x
Hybotinae	in flight	
Tachydromiinae	on solid substratum	
Brachystomatinae	?	?
Ceratomerinae	?	?
Tricopezinae	?	?
Microphoridae	in flight	x
Dolichopodidae	in flight	x

of the Empididae (Clinocerinae and Hemerodromiinae) as well as two subfamilies of the Hybotidae (Hybotinae and Tachydromiinae) may be considered as entirely predatory, the remaining families and subfamilies are both predators and pollen or nectar feeders. The Dolichopodidae are entirely predators apart from the genus *Hercostomus* of which species are nectar feeders (LAURENCE, 1953). The Microphoridae (genus *Microphorus*) are generally predators but also often found on flowers (CHVALA, 1983) but we do not know if they are pollen or nectar feeders. The Hybotidae genera *Anthalia*, *Allanthalia* and *Euthyneura* are pollen or nectar feeders but one species (at least), *Anthalia bulbosa*, is known to feed on pollen (DOWNES & SMITH, 1969), the remaining Hybotidae are entirely predators (CHVALA, 1983). The Oreogetoninae genera *Iteaphila* and *Anthepiscopus* are pollen or nectar feeders whereas *Hormopeza* species are predators (CHANDLER, 1972). The Empidinae are nectar feeders but during the mating period males hunt other insects which are offered to females as a nuptial gift. Three remarks are necessary, (1) males never feed preys which they have caught, (2) in the genus *Hilara*, the gift can be a simple vegetal fragment not edible to the female (TREHEN, 1965), (3) species of this genus have rarely been observed outside the habitat (generally places with presence of water: river, lake or simple puddle) where individuals hunt and mate, consequently evidence of their feeding habits is lacking. The feeding habits of Tricopezinae, Ceratomerinae, Brachystomatinae and Atelestidae are almost entirely unknown on account of the scarcity of their species in the nature. CHVALA (1983) supposed that the Ceratomerinae are flower visitors because their proboscis is elongated, but the presence of a morphological character is not unequivocal evidence of the existence of a behavior.

Among the Empidoidea, it is possible to distinguish four chief classes, species entirely predators (Hybotinae, Tachydromiinae, Clinocerinae and Hemerodromiinae), species entirely flower visitors (*Hercostomus*, *Anthalia*, *Allanthalia* and *Euthyneura*), species both predators and flower visitors (*Microphorus*) and the flower visiting species in which predation is only performed by males and during the mating period (Empidinae). Among the predators, the hunting can take place in flight (Dolichopodidae, Microphoridae, Hybotinae, Ocydromiinae, Oreogetoninae, Clinocerinae and Empidinae) or on the ground (Tachydromiinae and Hemerodromiinae).

Swarming habits

Swarming is a well known habit in many groups of Diptera (GRUHL, 1955; MCALPINE & MUNROE, 1968; DOWNES, 1969; CHVALA, 1990) especially in the Empidoidea. Indeed, 5 families or subfamilies of empidoïds display this behavior; the Microphoridae, Atelestidae, Ocydromiinae, Oreogetoninae and Empidinae. The remaining Empidoidea have never been observed to form swarms (Dolichopodidae, Hybotinae, Tachydromiinae, Clinocerinae and Hemerodromiinae) or are insufficiently known (Brachystomatinae, Ceratomerinae and Tricopezinae).

GRUHL (1955) distinguished synhesmic swarming from synorchesic swarming. The first is characterized by an unorganized mass of a large number of individuals resulting from mass emergence, the second forms coherent units characterized by an ordered flight (often species-specific) of several individuals termed true synorchesia. Gruhl also distinguished several evolutionary steps leading to this true synorchesia, chiefly the prosynorchesium (a pursuit flight of males from their perching places), the monorchesium (the hovering and dancing of isolated individuals) and the polyorchesium (the rhythmic alternation of dancing-perching-dancing of a

few individuals). Among the Empidoidea, it seems that the Empidinae form the polyorchesium swarms, whereas the other groups, especially Ocydromiinae, have generally observed in monorchesium swarming (CHVALA, 1983).

Swarming in the Empidoidea has always been linked to the meeting of sexes and thus to the mating. In fact, as CHVALA (1980) noted, it seems that this is characteristic of the Empidinae only. Indeed, in this group, males are seen in swarms with prey that are offered to females just before mating. Mating begins in the swarm and ends on a solid substratum. In the other Empidoidea forming swarms, hunting or mating have never been observed in swarms.

It seems therefore that, both structurally and functionally, swarms formed by the Empidinae are distinguishable from these of the Atelestidae, Microphoridae, Oreogetoninae and Ocydromiinae. That is why in table 2 we consider 3 cases among the superfamily, groups of which species never form swarms (no swarming activity), these for which swarming represents a monorchesium and in which hunting or mating has not been observed (swarms without mating), and these for which swarming represents a polyorchesium or true synorchesia and which are linked with both a predatory and mating activities (mating swarms).

Nevertheless, we will also consider the case where two attributes under two states are successively treated, presence and absence of swarms and beginning of mating in or outside swarms.

TABLE 2. — Swarming and mating habits in the Empidoidea. A question mark indicates an unknown state.

Taxa	No swarming activity	swarms without mating	Mating swarms
Atelestidae		x	
Oreogetoninae		x	
Clinocerinae	x		
Empidinae			x
Hemerodromiinae	x		
Ocydromiinae		x	
Hybotinae	x		
Tachydromiinae	x		
Brachystomatinae	?	?	?
Ceratomerinae	?	?	?
Tricopezinae	?	?	?
Microphoridae		x	
Dolichopodidae	x		

FORMER EVOLUTIONARY HYPOTHESES

Feeding habits

Predatory activity has always been considered ancestral for the Empidoidea (CHVALA, 1983) for at least three reasons, (1) it is a very widespread habit in the superfamily, the flower visitor species being only found in a few genera and one subfamily, (2) predation is considered the basal feeding habit of the Asiloidea and Empidoidea, (3) oldest known fossil of Empidoidea is

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┌─────────────────────────────────┐        ┌─────────────────────┐
│          FIRST STAGE            │        │   PRIMITIVE TAXA    │
│                                 │        └─────────────────────┘
│ > Presence of swarms.           │                  │
│ > Beginning of mating in swarms,│                  │
│   ending on a solid substratum. │                  │
│ > Significance of swarms: adapt.│                  │
│   for the meeting of sexes.     │                  │
└─────────────────────────────────┘                  │
              │                                       │
              ▼                                       │
┌─────────────────────────────────┐                  │
│          SECOND STAGE           │                  │
│                                 │                  │
│ > Presence of swarms.           │                  │
│ > The whole process of mating on a               │
│   solid substratum.             │                  │
│ > Significance of swarms: unknown│                 │
│   or relict swarms.             │                  │
└─────────────────────────────────┘                  │
              │                                       ▼
              ▼                            ┌─────────────────────┐
┌─────────────────────────────────┐        │  SPECIALIZED TAXA   │
│          THIRD STAGE            │        └─────────────────────┘
│                                 │
│ > No swarming activity.         │
│ > The whole process of mating on a
│   solid substratum.             │
└─────────────────────────────────┘
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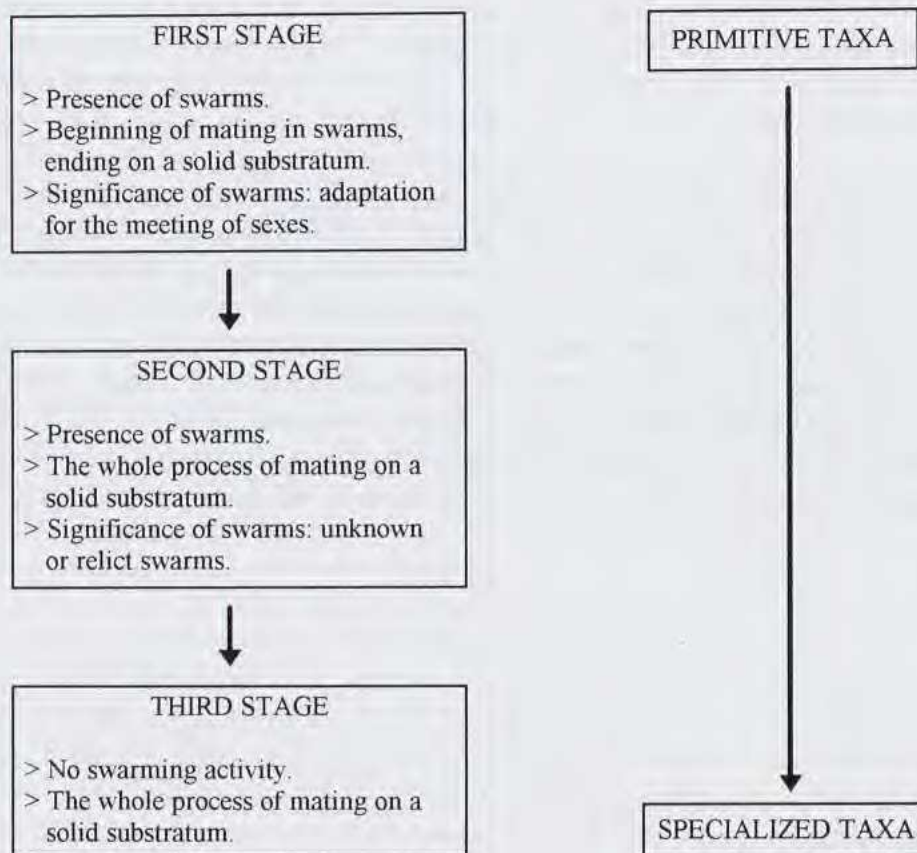
Fig. 3. — Model of the evolution of swarming in Diptera (after McAlpine & Munroe, 1968; Downes, 1969; Chvala, 1983).

dated from 160 millions years (middle Jurassic) (Usachev, 1968) before the rise of the angiosperms.

The fact that predation is very widespread in the superfamily is not evidence of its supposed ancestral origin. Such hypothesis can be compared to the ingroup distribution criteria used in phylogeny to establish the polarity of characters. Now we know that this criteria is not valuable. On the other hand, in the Asiloidea, only the Asilidae are predatory, and the habits of the Asiloidea could be informative in this context if the Empidoidea and Asiloidea are sister groups, but the sister-group of the Empidoidea is the Cyclorrhapha (Cumming *et al.*, 1995).

For these reasons, it seems justified to test the hypothesis of plesiomorphy of predation for the Empidoidea. We will also test the hypothesis that predation in flight is ancestral to predation on the ground.

Swarming habits

The significance and evolution of swarms in the Diptera have been studied in several papers, GRUHL (1955), MCALPINE & MUNROE (1968), DOWNES (1969) and CHVALA (1976, 1980, 1990). From these works, we can present consensus which may be summarized in two points, (1) swarming is ancestral for the Diptera in general and each taxon of Diptera which presents this behavior in particular, (2) the original function of swarming is the meeting of sexes, whereas the mating or hunting on a solid substratum is a specialized activity. This consensus is the result of two observations which have been detailed by MCALPINE & MUNROE, (1) swarming exists in the main lineages of Diptera, nevertheless being more widespread in the Nematocera (reputed primitive) than in the Brachycera (reputed specialized), (2) for Diptera in particular and insects in general which present a swarming activity, the meeting of sexes and the beginning of mating often take place in the swarms. To summarize these hypotheses (MCALPINE & MUNROE, 1968: 1167) "The remarkable correlation between swarming and mating habits [...] in the phyletically distant Diptera, is a clear indication that swarming and coupling in flight are basic to a dipterous condition".

Nevertheless, there exists a large number of Diptera forming swarms of which the function remains unknown. As presented earlier, no swarming Empidoidea has been observed to mate in the swarms except species of the subfamily Empidinae. Several unconvincing hypotheses have been proposed to explain the significance of these swarms (for example see PAJUNEN, 1980). CHVALA (1983) proposed that these swarms are relicts of an ancestral behavior in which mating is correlated with swarming, mating activity of these groups would have been transferred on a solid substratum and swarms would be without particular significance.

These hypotheses can be summarized in an evolutionary model (Fig. 3) that is applies to the whole order Diptera. Among the Empidoidea, families and subfamilies can be affiliated to one stage of model: (first stage) Empidinae: meeting of sexes and beginning of mating in the swarm, swarms are an adaptation for the meeting of sexes; (second stage) Atelestidae, Oreogetoninae, Ocydromiinae and Microphoridae: meeting of sexes and mating transferred on a solid substratum, swarms as relict of ancestral behavior; (third stage) Dolichopodidae, Hybotinae, Tachydromiinae, Clinocerinae and Hemerodromiinae: meeting of sexes and mating on a solid substratum, loss of the ability to form swarms.

THE TESTS OF EVOLUTIONARY HYPOTHESES

The reconstruction of phylogenies is independent from most process theories (ELDREDGE & CRACRAFT, 1980), that is why the optimization method, as described by BROOKS & MCLENNAN (1991) among others, allows evolutionary models to be tested objectively. The optimization consists of mapping the previously defined attributes on the phylogeny and follow their evolution on the cladogram with respect of the parsimony principle.

Feeding habits

Predator – Flower visitor. Feeding habits were scored in two states, predator or flower visitor. After optimization, the cladogram (Fig. 4) shows that predation is plesiomorphic for all the Empidoidea but also for the clades [Dolichopodidae + Microphoridae], Hybotidae and Empididae. The flower visiting habit is apomorphic for the Empidinae, predation having only been conserved during the mating period. The flower visiting habit has appeared independently in

several other lineages of Empidoidea, but two cases must be distinguished. The first is represented by the Dolichopodidae, Ocydromiinae and Oreogetoninae, for which some genera became flower visitors (see the chapter "attributes"), and the second is represented by species of the genus *Microphorus* (Microphoridae) which are both predators and flower visitors. It is possible to consider that the flower visiting habit has recently appeared in this family. The traditional model is therefore corroborated by the phylogenetic test.

Predation in flight – Predation on solid substratum. The attribute (predation) has been considered under two states (in flight or on solid substratum). After optimization, the phylogeny (Fig. 5) shows that predation in flight is ancestral for all the Empidoidea and the clades [Dolichopodidae + Microphoridae], Hybotidae and Empididae. Even if predation in flight is plesiomorphic, it must be noted that this is considerably diversified and specialized in present taxa, for instance females of some microphorids of the genus *Microphorus* catch other insects in the spider webs; the Clinocerinae and males of the genus *Hilara* (Empidinae) hunt on the surface of water, the second of these wrap up prey in a silk balloon which is presented to the females just before mating as a nuptial gift. To summarize, different forms of hunting in flight observed among the Empidoidea are apomorphic for each considered taxon.

Hunting on a solid substratum (on the ground or on a leaf for example) is apomorphic for the Tachydromiinae (Hybotidae) and Hemerodromiinae (Empididae) (Fig. 5). Thus it is a very specialized type of predation that appeared by convergence in these two subfamilies. Species in these two subfamilies also possess a convergently specialized morphology where the thorax is elongated and the fore and sometimes middle legs are raptorial with elongated coxae, thick femora, and bent tibiae (Fig. 1). These morphological characters are likely to be an adaptation for predation on a solid substratum because Hemerodromiinae and Tachydromiinae are respectively the only taxa in Empididae and Hybotidae to present them. Tachydromiinae and Hemerodromiinae are therefore a remarkable example of both morphological and behavioral convergences. Of course, this does not mean that the presence of such characters involves such behaviors, unfortunately this "rule" is often applied in evolutionary biology and cases of exaptation are often overlooked.

Swarming habits

Presence/Absence of swarms. According to optimization, two equally parsimonious patterns (4 steps) (Figs 6, 7) have been obtained. In both cases, swarming is plesiomorphic for all the Empidoidea, [Dolichopodidae + Micophoridae], [Atelestidae + Hybotidae + Empididae], and for the Hybotidae and Empididae themselves, whereas the absence of swarming is apomorphic for the Dolichopodidae and [Hybotinae + Tachydromiinae]. In the Empididae, the situation is more complex because, although in the first and second patterns, swarming appears as ancestral for the family, two cases must be considered for the clade [Clinocerinae + Empidinae + Hemerodromiinae]. In the first pattern (Fig. 6), swarming is plesiomorphic for this clade but also the [Empidinae + Hemerodromiinae], the loss of this behavior occurring twice, once in the Clinocerinae and a second time in the Hemerodromiinae. Swarming remains therefore plesiomorphic for the Empidinae whereas the absence of swarming is apomorphic for the Clinocerinae and Hemerodromiinae. In the second pattern (Fig. 7), the absence of swarming is ancestral for the [Clinocerinae + Empidinae + Hemerodromiinae] with a reversion for the Empidinae, swarming being therefore apomorphic for this subfamily.
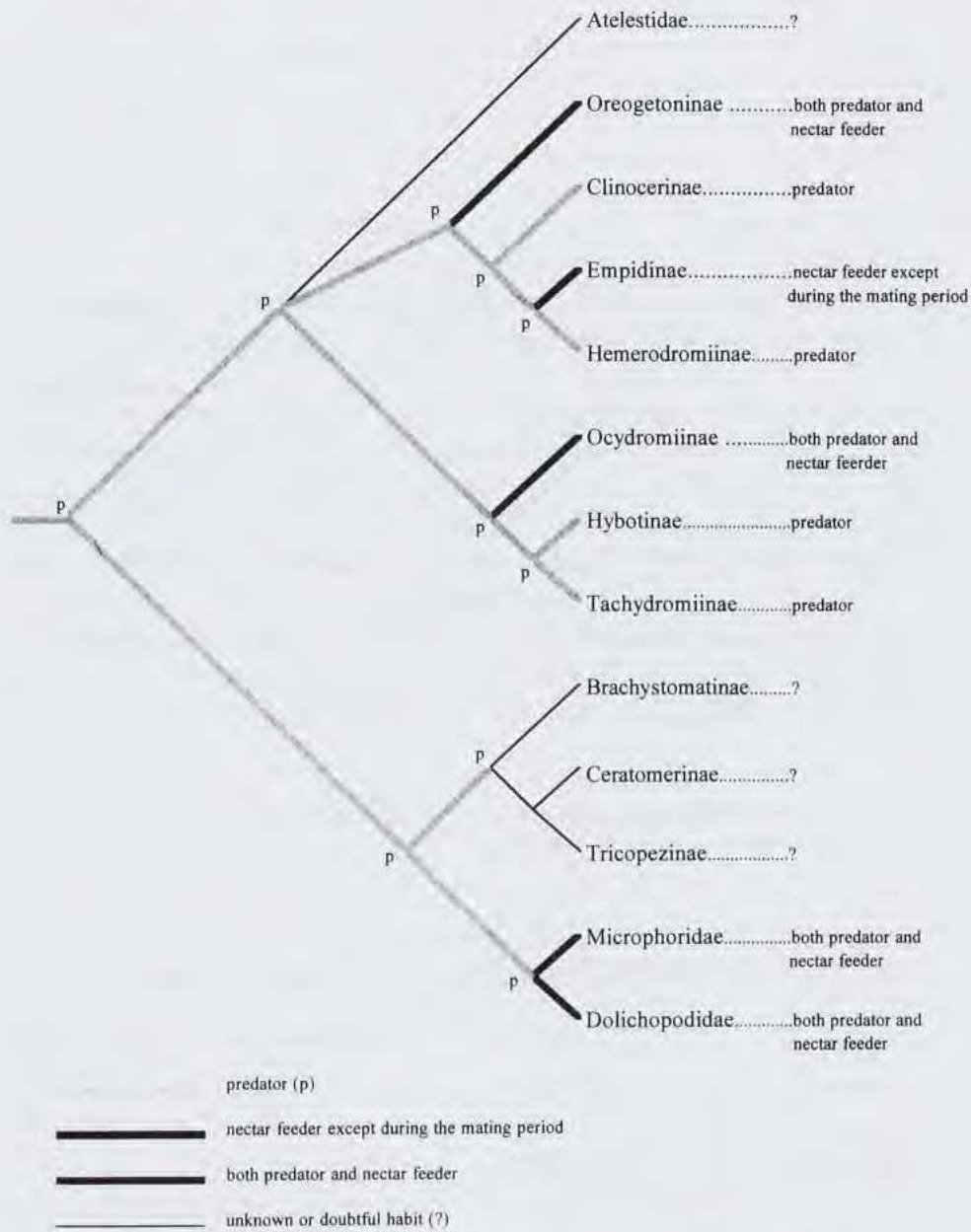
FIG. 4. — Cladogram of Empidoidea showing optimization of feeding habits.

Mating in/outside swarms. Mating in swarms being specific of Empidinae, this behavior is apomorphic for this group (Fig. 8). Conversely mating outside swarms is plesiomorphic for all the Empidoidea and all clades of the phylogeny including the terminal taxa apart from, of course, the Empidinae.

Swarming in Empidinae: exaptation or adaptation to the meeting of sexes? The cladistic tests of adaptation hypotheses have been reviewed by CODDINGTON (1988) and GRANDCOLAS *et*
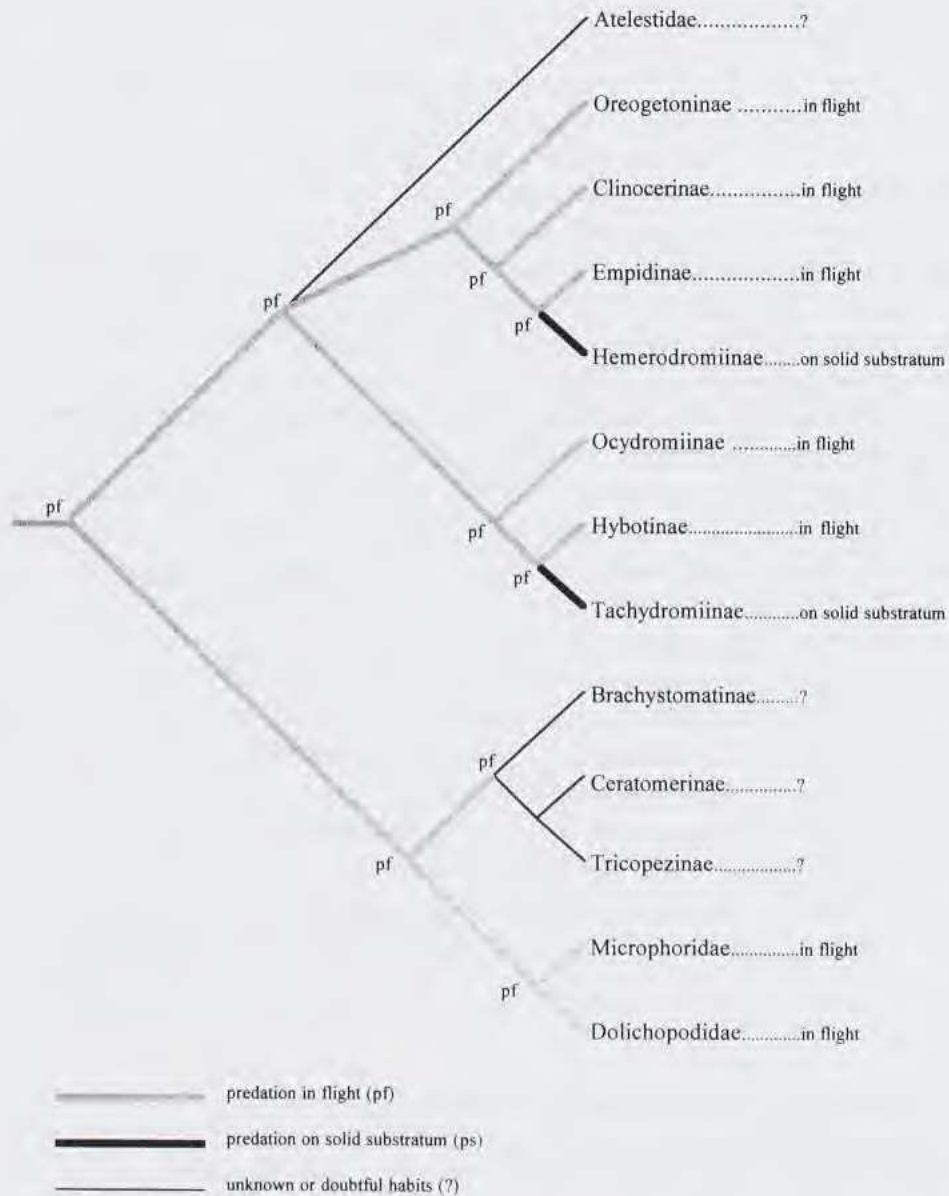
Fig. 5. — Cladogram of Empidoidea showing optimization of type of predation.

al. (1994). To summarize, a character is an adaptation for a given taxon if it has appeared in this taxon with the additional assumption of its selective value.

If we combine the previous result (mating in swarms as apomorphic for the Empidinae) with both equally parsimonious patterns for the first attribute (presence or absence of swarms) then two cases are possible for the Empidinae, (1) swarming is plesiomorphic and has been inherited from the ancestor of the Empidoidea (and swarms formed by different Empidoidea are homologous) for which the phylogeny shows mating did not take place in the swarms (Fig. 6).

They therefore had a different function that was not to allow the meeting of sexes. Consequently, swarming in the Empidinae is an exaptation (GOULD & VRBA, 1982) to the meeting of sexes. (2) Swarming is apomorphic for the Empidinae (Fig. 7) and it appeared with the subfamily (swarms formed by the Empidinae are therefore not homologous with these formed by some other Empidoidea). The mating in swarms arising in the Empidinae, the adaptive hypothesis that swarming evolved for the meeting of sexes is corroborated by the phylogeny.

To summarize (Table 3): according to both patterns, the traditional model is refuted in two points, (1) the ancestral state is not the formation of mating swarms but the formation of swarms of which the function is unknown, the mating taking place on a solid substratum (or may be in flight but not in swarm), (2) mating in swarms is an apomorphic behavior that appeared with the Empidinae.

In addition, the pattern 1 refutes the adaptation hypothesis of swarming for the meeting of sexes in Empidinae whereas the pattern 2 corroborates it. Finally, the absence of swarms as apomorphic character is corroborated for Dolichopodidae and [Hybotinae + Tachydromiinae] by both patterns and Hemerodromiinae and Clinocerinae by the first pattern but refuted by the second because in this case the loss of the ability to form swarms took place for the ancestor of the clade [Clinocerinae + Empidinae + Hemerodromiinae].

Is it possible to choose between exaptation and adaptation for the formation of swarms in the Empidinae? In fact we can only consider one attribute (swarming) under three states (absence – swarming without mating – mating swarms) rather than two attributes (swarming – mating)

TABLE 3. — Former evolutionary hypotheses and their tests by two phylogenetic patterns (optimizations on the cladogram). *: in the empidids, the corroboration is only true for the clade [Clinocerinae + Empidinae + Hemerodromiinae] with a reversion for the Empidinae.

Former evolutionary hypotheses	According to pattern 1	According to pattern 2
Mating swarms : plesiomorphic	Refuted	Refuted
Swarms without mating: relict from mating swarms	Refuted	Refuted
Mating swarms: adaptation to the meeting of sexes (in Empidinae)	Refuted	Corroborated
No swarming activity: apomorphic	Corroborated	Corroborated *

under two states (respectively absence – presence and in or outside swarms) for the reasons explained in the chapter "Attributes".

Absence of swarms – swarming without mating – mating swarms. After optimization, a pattern (Fig. 9) as parsimonious (4 steps) as the previous ones has been found. Swarming

Atelestidae...................swarming activity

Oreogetoninae ....swarming activity

Clinocerinae...............no swarming activity

Empidinae.................swarming activity

Hemerodromiinae........no swarming activity

Ocydromiinae ....swarming activity

Hybotinae........................no swarming activity

Tachydromiinae............no swarming activity

Brachystomatinae.........?

Ceratomerinae...............?

Tricopezinae.................?

Microphoridae..............swarming activity

Dolichopodidae............no swarming activity

——————— swarming activity (s)

——————— no swarming activity (ns)
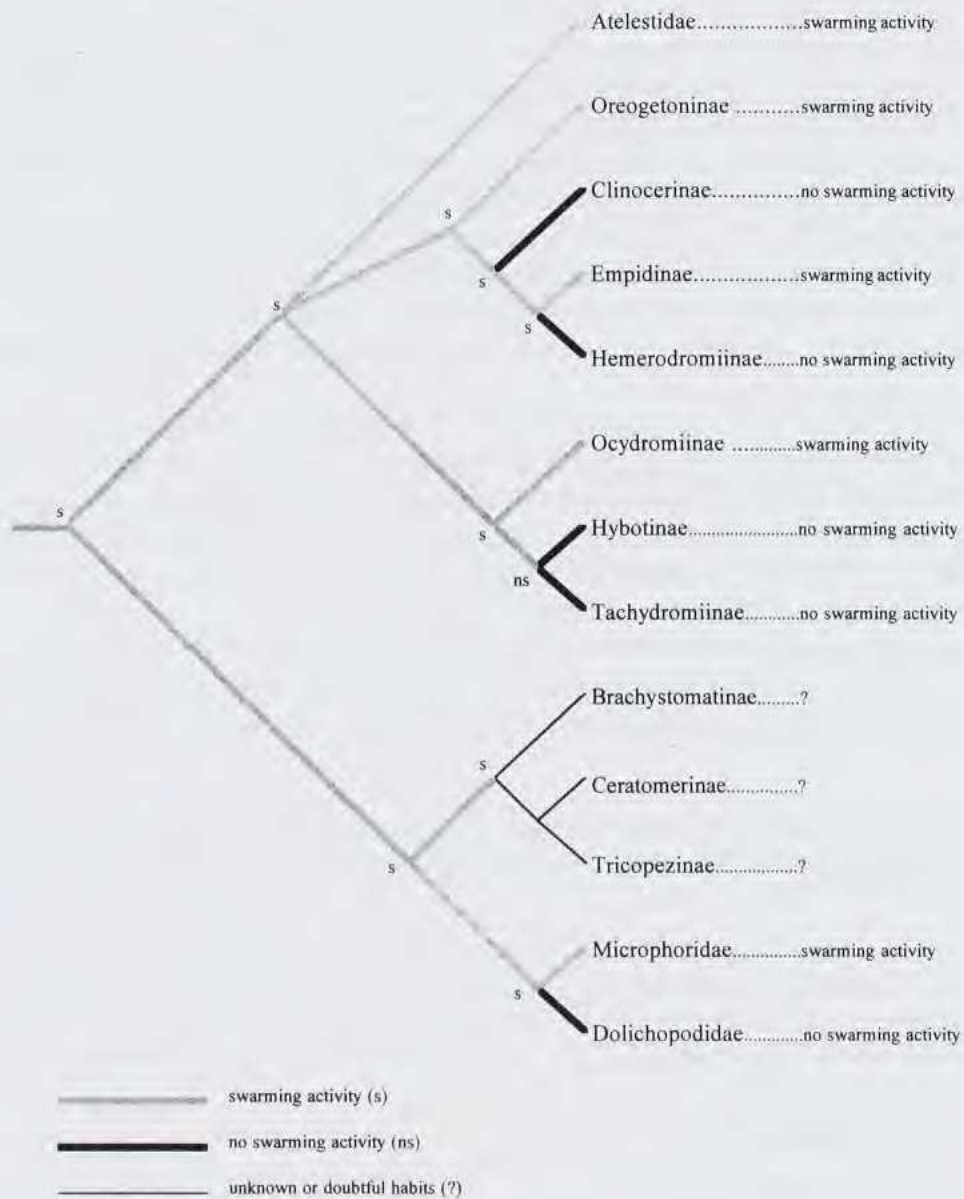
——————— unknown or doubtful habits (?)

FIG. 6. — Cladogram of Empidoidea showing optimization of swarming habits. First pattern.

without mating is plesiomorphic for the Empidoidea, [Dolichopodidae + Microphoridae], Atelestidae, Hybotidae and Empididae, the absence of swarms is apomorphic for the Dolichopodidae, [Hybotinae + Tachydromiinae] and [Clinocerinae + Empidinae + Hemerodromiinae]. On the other hand, the Empidinae are the only Empidoidea which form mating swarms. This behavior is therefore apomorphic for this subfamily and as in the pattern 2, the adaptation hypothesis for swarming to the meeting of sexes is corroborated.
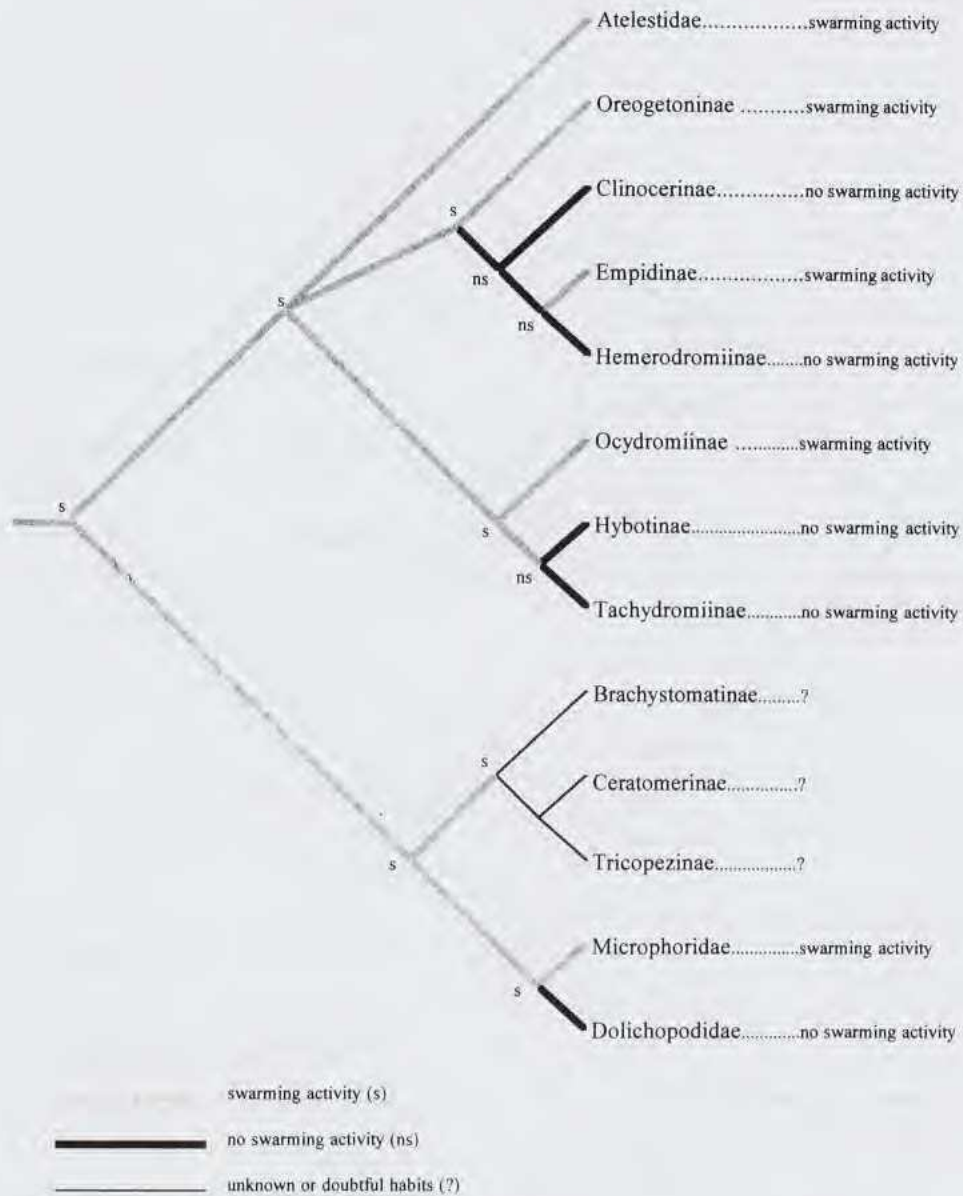
Fig. 7. — Cladogram of Empidoidea showing optimization of swarming habits. Second pattern.

DISCUSSION

Swarms formed by the Empidinae are structurally (according to the GRUHL classification, 1955) different from those formed by some other Empidoidea. Within these swarms, the Empidinae show a succession of behaviors (hunting, meeting of sexes, nuptial gift, beginning of mating) never observed in any other Empidoidea. In the Empidinae, swarming and mating seem therefore correlated, this pleads in favor of the consideration of one attribute under three states (no swarming activity, swarming without mating and mating swarms). Nevertheless the

Atelestidae.................mating oustside swarms

Oreogetoninae............mating outside swarms

Clinocerinae...............mating outside swarms

Empidinae..................mating in swarms

Hemerodromiinae........mating outside swarms

Ocydromiinae ....mating outside swarms

Hybotinae.......................mating outside swarms

Tachydromiinae...........mating outside swarms

Brachystomatinae.........?

Ceratomerinae..............?

Tricopezinae.................?

Microphoridae..............mating outside swarms

Dolichopodidae...........mating outside swarms

▬▬▬▬▬ mating in swarms

------------ mating outside swarms (mo)

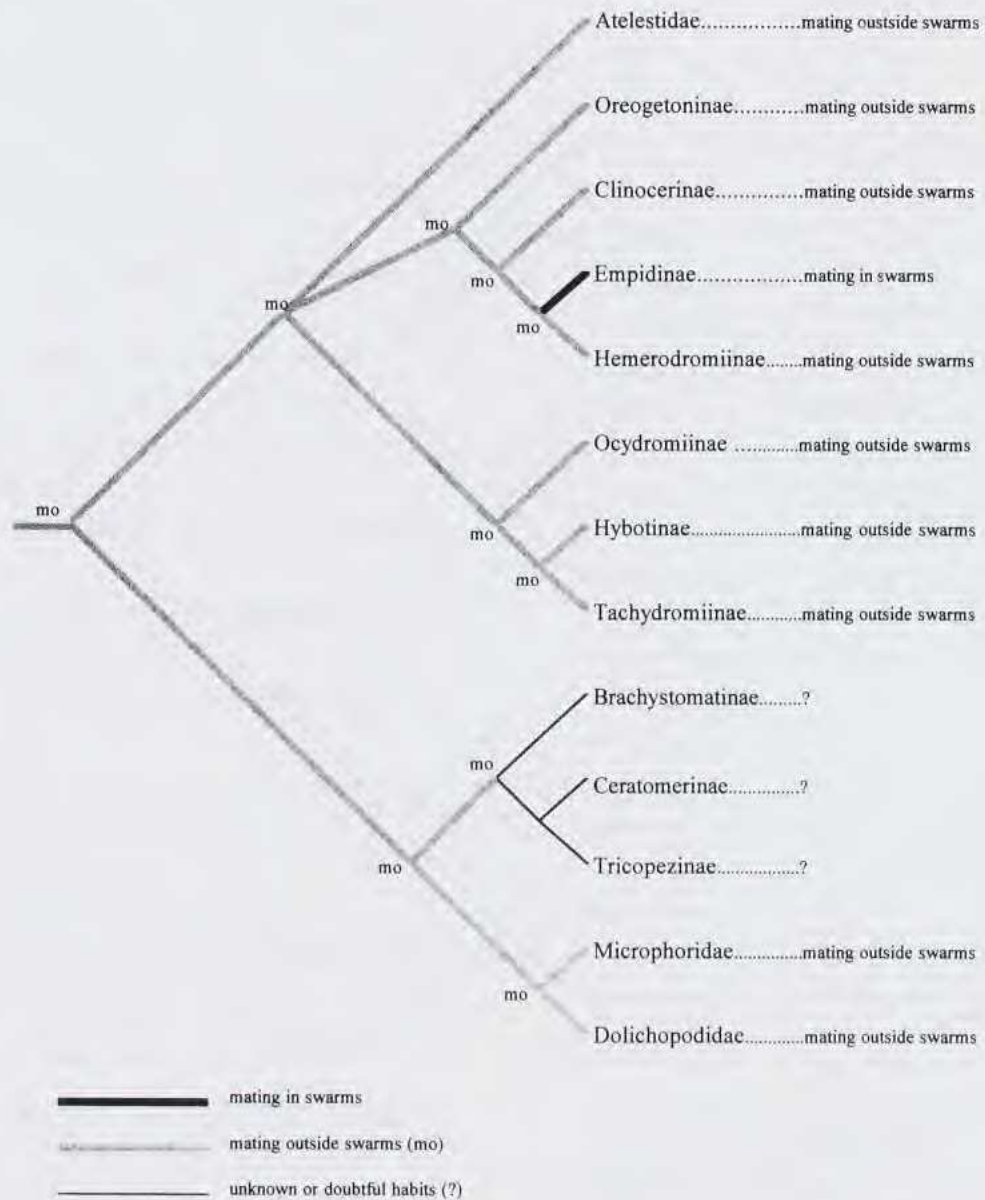▬▬▬▬▬ unknown or doubtful habits (?)

FIG. 8. — Cladogram of Empidoidea showing optimization of type of mating.

consideration of two attributes allows two patterns of which one gives results analogous with those obtained with one attribute. Consequently it seems that the following conclusions force themselves:

1) Swarming and mating outside swarms are plesiomorphic for the Empidoidea.

2) The absence of swarms in some Empidoidea is apomorphic for three clades, Dolichopodidae, [Hybotinae + Tachydomiinae] and [Clinocerinae + Empidinae + Hemerodromiinae].

Atelestidae................swarms without mating

Oreogetoninae............swarms without mating

Clinocerinae...............no swarming activity

Empidinae..................mating swarms

Hemerodromiinae........no swarming activity

Ocydromiinae ....swarms without mating

Hybotinae......................no swarming activity

Tachydromiinae............no swarming activity

Brachystomatinae.........?

Ceratomerinae..............?

Tricopezinae.................?

Microphoridae...............swarms without mating

Dolichopodidae............no swarming activity

swm — mating swarms

swm — swarms without mating (swm)

ns — no swarming activity (ns)
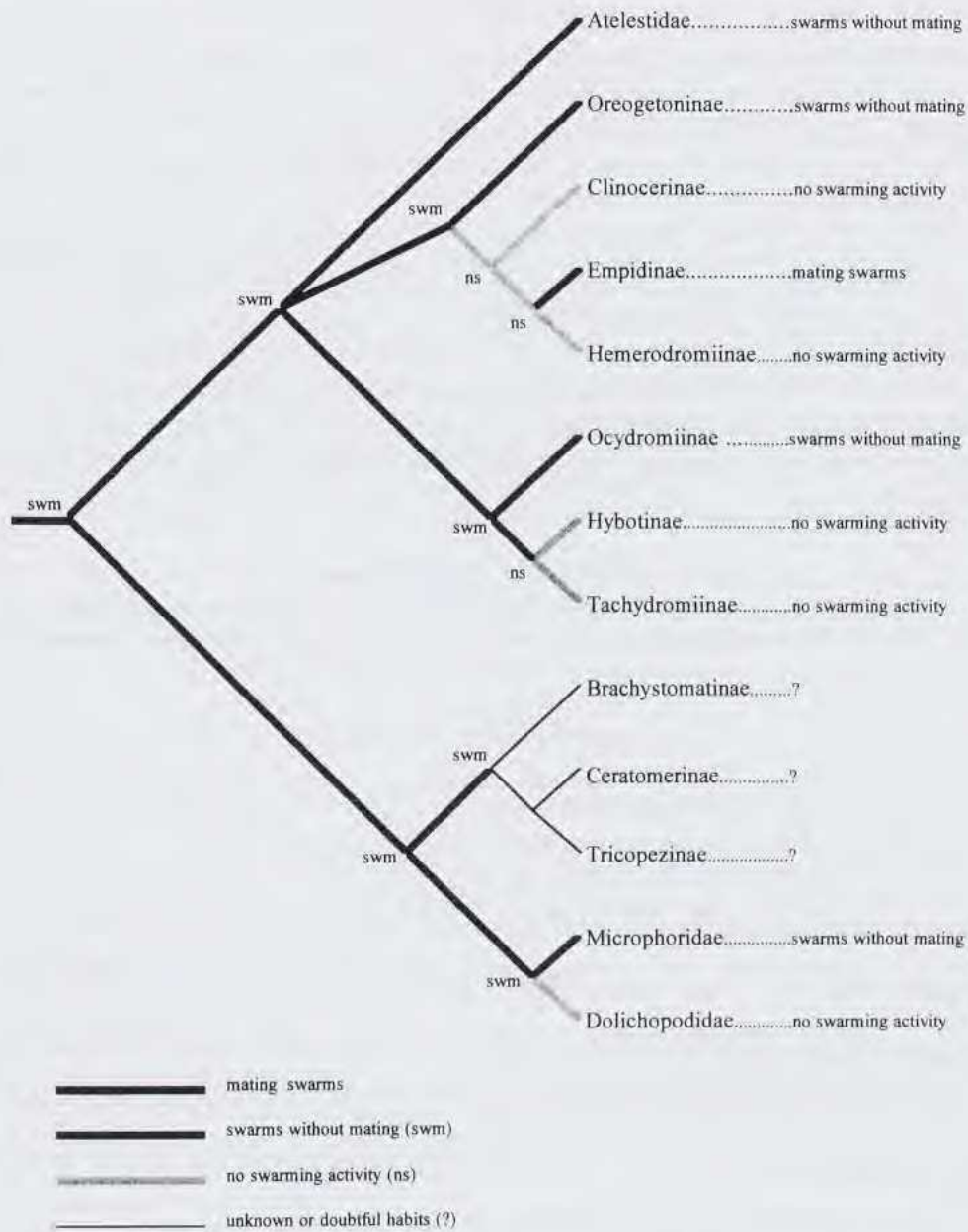
? — unknown or doubtful habits (?)

Fig. 9. — Cladogram of Empidoidea showing optimization of both swarming and mating.

3) Mating swarms are apomorphic for the Empidinae but not homologous with swarms formed by other Empidoidea. Thus they cannot be integrated to a global evolutionary model and thus do not form the basis of this model as it has always been presented. On the other hand, in the Empidoidea, swarming without mating cannot be considered a relict from mating swarms.

4) The adaptation hypothesis of swarming to the meeting of sexes is corroborated for the Empidinae without, of course, prejudging of the selective value of this behavior.

CONCLUSION

The optimization of characters on the phylogeny leads to refutable results and is the only objective test of evolutionary models because of its independence from these models. Thus systematics must not be only considered as the science of inventories, descriptions and classifications of taxa in predictive systems, but also as the science of explanatory framework for character evolution.

This method is therefore employed herein for the first time for the Empidoidea, but important advances remain to be achieved in both phylogeny and ethology of the Empidoidea before to offer more stable evolutionary hypotheses.

Finally, focusing on the phylogenetic patterns in the subfamily Empidinae is probably the most interesting perspective. CUMMING (1994) proposed an evolutionary model for this group with reference to sexual selection. Using phylogeny, it will be therefore possible to test this model and other hypotheses relating the origin and evolution of both nuptial gift and female ornementations.

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APPENDIX 1. — List of characters and Matrix. In brackets, bold-faced and italic types indicate respectively the number of the page and the number of the character in the original work.

1. Maxillary lacinia absent: 1, present: 0 (CHVALA, 1983: **61**, *12*, WIEGMANN *et al.*, 1993: **66**, *9*).
2. Palpi connected to palpifer: 1, attached to stipites: 0 (CHVALA, 1983: **61**; *13*; WIEGMANN *et al.*, 1993: **66**, *8*).
3. Prokatepisternum fused with the basisternite: 1, isolated: 0 (CHVALA, 1983: **61**, *10*; WIEGMANN *et al.*, 1993: **66**, *12*).
4. Mesoanepimeral suture present and forming a ¼ - half of circle: 1, present and forming a ¼ of circle, absent: 0 (ULRICH, 1971, *Figs 3, 4, 5, 44, 45*; 1994: **230**).
5. Two discal veins: 1, three discal veins: 0 (CHVALA, 1983: **61**; *8*; WIEGMANN *et al.*, 1993: **68**, *21*).
6. Front tibiae with tubular gland: 1, tubular gland absent: 0 (CHVALA, 1983: **61**; *11*; WIEGMANN *et al.*, 1993: **70**, *28*).
7. male cerci sclerotized: 1, not sclerotized: 0 (ULRICH, 1975; CUMMING *et al.*, 1995: **133**, *12*).
8. Rotation of male hypopygium between 45°and 90°: 1, Hypopygium without rotation: 0 (CHVALA, 1983: **61**, *3*; CUMMING *et al.*, 1995: **133**, *14*).
9. Rotation of both male hypopygium and segments 7 and 8: 1, Hypopygium and segments 7 and 8 without rotation: 0 (CUMMING *et al.*, 1995: **133**, *15*).
10. Bacilliform sclerite and hypandrium fused: 1, no fused: 0 (CUMMING *et al.*, 1995: **134**, *16*).
11. Sternite 8 of female articulated or fused with tergite 8: 1, well separated: 0 (SINCLAIR, 1995: **718**, *1*).
12. female cerci sclerotized: 1, not sclerotized: 0 (SINCLAIR, 1995: **718**, *2*).
13. Tergite 7 of female with a fringe of bristles on the posterior margin: 1, without fringe of bristles: 0 (SINCLAIR, 1995: **719**, *3*).
14. female cerci upright: 1, horizontal: 0 (SINCLAIR, 1995: **719**, *4*).
15. Acanthophorites absent: 1, present: 0 (SINCLAIR, 1995: **668**).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Atelestidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oreogetoninae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Clinocerinae	0	0	1	1	0/1	0	0	0	0	0	0	0	0	0	1
Empidinae	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1
Hemerodromiinae	0	0	1	1	0/1	0	1	0	0	0	0	0	0	0	1
Ocydromiinae	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1
Hybotinae	1	1	0	0	1	1	0	1	0	0	0	0	0	0	1
Tachydromiinae	1	1	0/1	0	1	1	0	1	0	0	0	0	0	0	1
Brachystomatinae	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0
Ceratomerinae	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0
Tricopezinae	0	0	0/1	1	0	0	0	0	0	0	1	1	1	1	0
Microphoridae	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
Dolichopodidae	0	0	0/1	0	1	0	0	0	1	1	1	1	0	0	0